Impact of hurricane Dean on coral reef benthic and fish structure of Martinique, French West Indies

by

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ABSTRACT. - The impact of hurricane Dean was assessed on the Caribbean southern reef of Martinique (French West Indies). A line-intercept transect method was used to assess benthic communities and an underwater visual census technique was employed on a 50 m long transect to evaluate fish assemblages. Univariate and multivariate statistical tools were used for data analysis. Correlated changes of benthic and fish communities were found along the 15 months post-hurricane. The effects of hurricane Dean can be divided into (1) immediate and rapid effects and (2) gradual effects. The former has been linked to the rapid destruction and reorganization of the reef habitat. A significant decline of the mean coral cover (from 37% to 23%) associated with a rapid colonization by macroalgae communities was recorded. The significant benthic community modifications changed fish species richness, abundance and community structure. The second effect relates to the ability of reef species to adapt to new environmental conditions. Populations of two damselfish species (Pomacentridae) have taken advantage of reef destruction to expand their territory and favoured the spread of the macroalgae community. As a result, the fish community was significantly modified while the habitat complexity was considerably reduced due to digitate coral destruction.

RÉSUMÉ. - Impact du cyclone Dean sur la structure benthique et ichtyologique récifale de Martinique (Antilles françaises).

L'impact du cyclone Dean a été étudié sur le récif sud de la Martinique (Antilles françaises). Les communautés benthiques ont été étudiées grâce à la méthode du "ligne-intercept" et le peuplement de poissons analysé à partir de recensements visuels. Le traitement des données a été réalisé à l'aide d'outils statistiques univariés et multivariés. Les résultats ont montré des modifications des communautés benthiques et ichtyologiques jusqu'à 15 mois après le passage du cyclone. Cet événement climatique a eu un impact en deux temps avec (1) des effets rapides et immédiats et (2) des effets progressifs à moyen terme. Le premier impact est lié à la destruction rapide et la réorganisation de l'habitat récifal. Une baisse significative de la couverture corallienne moyenne (de 37% à 23%) associée à une colonisation rapide par les communautés algales a été observée. Les changements significatifs des communautés benthiques se sont accompagnés de modifications de la richesse spécifique, des densités et de la structure ichtyologiques. Le second impact provient de la capacité des espèces récifales à s'adapter à de nouvelles conditions environnementales. La restructuration de l'habitat récifal a eu un impact significatif sur le peuplement de poissons, notamment sur deux espèces de demoiselles (Pomacentridae).

Key words. - Pomacentridae - French West Indies - Martinique - Coral damage - Algae bloom - Fish community - Hurricane Dean.

The decline of coral reefs worldwide has dramatically increased over the past 30 years (Wilkinson, 2008). Storms, rainfall and terrestrial run-off, sedimentation, disease, eutrophication, destructive fishing practices and overfishing, coral mining, and physical damages from anchoring are important natural and anthropogenic disturbances affecting coral community structure (Grigg and Dollar, 1990; Connell *et al*., 1997; Lapointe, 1997; Hodgson, 1999; Nyström *et al*., 2000; Nyström and Folke, 2001; Bellwood *et al*., 2004; Lapointe *et al*., 2004; Chabanet *et al*., 2005; Wilson *et al*., 2006), and positively or negatively impact the associated fish and invertebrate populations. Most of the Caribbean coral reefs have shifted from their initial coral dominant status to macroalgae or algal turf (McCook, 1999; McManus and Polsenberg, 2004) due to the cumulative impacts of these disturbances. The island of Martinique has been continuously subjected to these perturbations and the coastal marine ecosystems have significantly degraded since the 80's (Bouchon and Laborel, 1986). The mass mortality of *Acropora* spp. during the 70's and the plague of *Diadema antillarum* (Philippi, 1845) in 1982-1984 were also observed in Martinique (Gladfelter, 1982; Bythell and Sheppard, 1993; Hughes, 1994; Aronson and Precht, 2001) modifying the ecology of the reefs in the area.

The status of coral reef health in Martinique varies from location to location and ranges from healthy to highly degraded (Legrand, unpubl. data). The demographic increase in Martinique (346 hab.km^2) and the subsequent urbanization are probably important factors. Agricultural practices and industrial discharge promote eutrophication and hyper

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sedimentation, principally in the bays. The consequence on shallow waters communities is the fast colonization of dead coral by macroalgae (Littler and Littler, 1984; Littler *et al*., 1992), which can in turn prevent the settlement of coral larvae (Titlyanov *et al*., 2005; Box and Mumby, 2007). During the summer and fall of 2005, elevated sea surface temperatures (> 30°C, NOAA, 2009) in the Caribbean caused a mass coral bleaching episode which resulted in 15% coral loss in Martinique (Legrand *et al*., 2008) followed by a disease outbreak, resulting in another 15% loss by June 2006 (Maréchal, unpubl. data).

Martinique is hit by hurricanes every 15 years on average, which is low compared to other Caribbean islands. The rarity of such events has never provided an opportunity to study their effect on Martinique reefs. The impacts of hurricanes on coral reefs can be different according to the storm path, strength, velocity, and the wave height and direction (e.g., Bythell *et al*., 2000; Gardner *et al*., 2005). Damages to coral reefs vary consequently (Wilkinson and Souter, 2008) with cases of minimal impact (e.g., Fenner, 1991; Glynn *et al*., 1998) and cases of major degradation (e.g., Harmelin-Vivien and Laboute, 1986; Bries *et al*., 2004). However, while the number of hurricanes has remained relatively constant, it is suggested that their strength has increased in recent years due to global climate change (Walsh and Ryan, 2000; Webster *et al*., 2005). Hurricane Dean hit Martinique on the 18th of August, 2007 and severely damaged the island. The event generated a strong South-South East swell (7 m amplitude in the Ste-Lucia Channel) that impacted the Caribbean southern reefs of Martinique, usually protected from the eastern dominant swell. The objectives of this first study on the hurricane impacts in Martinique were (1) to assess the immediate effect of hurricane Dean on benthic and fish assemblages and (2) to track the changes of the reef communities after one year.

MATERIALS AND METHODS

Study site

Monitoring on several sites on the Southern Caribbean reef of Martinique showed that only one was heavily impacted by hurricane Dean. Therefore, the survey was conducted at this site, Jardin Tropical (14°27’18.7”N; 60°55’30.7”W; Fig. 1). The study was carried out over 20 months, beginning 3 months before hurricane Dean (April 2007), followed by three other campaigns in November 2007, April 2008 and November 2008. The survey was conducted on the reef crest (8 to 12 m depth) where the swell had the highest impact.

Experimental design

Benthic community structure

Benthic community composition was described using a line-intercept transect method (LIT). Six linear transects (50 m) were deployed at random along the reef crest at 8-12 m depth with 10 m between each transect. Habitat variables, including live coral, dead coral (bare dead coral substrate and fragments), sessile invertebrates (soft coral, sponges, zoanthids), algae (macroalgae, turf, cyanophycae, encrusting and erected calcareous algae) and sand, were

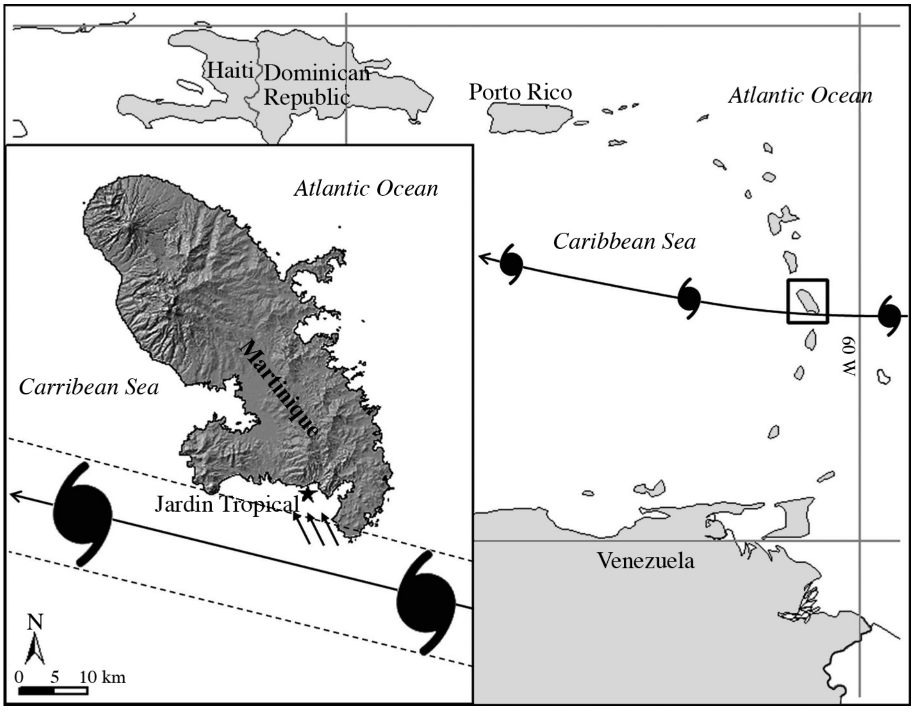

Figure 1. - Map of the study site, showing the location of Martinique in the Caribbean and the path of hurricane Dean. The detailed map indicates the location of the survey station (Jardin Tropical). The dotted lines represent the limits of the eye of the hurricane and the arrows indicate the swell direction.

Table I. - Benthic variables considered for the study and corresponding codes used for the different statistical analyses.

Benthic variables	Codes
Coral species (live coral)	COR
Agaricia sp. Lamarck, 1801	*Agaricia* sp.
Colpophyllia natans (Houttuyn, 1772)	*C. natans*
Diploria clivosa (Ellis & Solander, 1786)	*D. clivosa*
Diploria labyrinthiformis (Linnaeus, 1758)	*D. labyrinthiformis*
Diploria strigosa (Dana, 1846)	*D. strigosa*
Favia fragum (Esper, 1793)	*F.fragum*
Madracis decactis (Lyman, 1859)	*M. decactis*
Madracis mirabilis (Duchassaing & Michelotti, 1860)	*M. mirabilis*
Meandrina meandrites (Linnaeus, 1767)	*M. meandrites*
Millepora sp. Linnaeus, 1758	*Millepora* sp.
Montastraea annularis (Ellis & Solander, 1786)	*M.. annularis*
Montastraea cavernosa (Linnaeus, 1767)	*M. cavernosa*
Montastraea faveolata (Ellis & Solander, 1786)	*M.faveolata*
Montastraea franksi (Gregory, 1895)	*M.franksi*
Porites astreoides Lamarck, 1816	*P. astreoides*
Porites porites (Pallas, 1766)	*P. porites*
Siderastrea siderea (Ellis & Solander, 1786)	*S. siderea*
Bare dead coral	SUB
Rubble	RUB
Macroalgae	MALG
Turf	TURF
Encrusting calcareous algae	CALGenc
Erected calcareous algae	CALGere
Cyanophycae	CYANO
Sponges	SPON
Gorgonia	GORG
Zoanthids	ZOAN
Other invertebrates	INV

recorded every 0.50 m along the transect (100 points per transect) (Tab. I). The percentage occurrence of each benthic group, considered as percentage cover in this study, was calculated from these records.

Fish censuses

Fish community structure was surveyed using an underwater visual census technique adapted from the belt-transect method (Brock, 1954). Fish were censused over a four metre wide belt transect (50 x 4 m) at the same location as the benthos transect (e.g., Jones *et al*., 2004; Berumen and Pratchett, 2006) covering an area of 200 m^2. Individuals of all recognizable, non-cryptic (with some exceptions, Grammatidae, Holocentridae), and diurnally active species were recorded. Fishes were quantified by counting individuals of each species.

Six transect surveys were conducted during the daytime between 10:00 and 16:00, over two days to minimize daily variability of fish structure with environmental conditions.

Data analysis

Data transects were expressed as percentage cover of each benthic variable and the species richness of corals was evaluated. Fish densities were calculated as the total number of individuals per species divided by the total area surveyed and expressed per 200 m^2. Fish species were divided into trophic groups (planktivore, roving herbivore, territorial herbivore, sessile invertebrate feeder, mobile invertivore, omnivore, carnivore and piscivore) on published information (Floeter *et al*., 2004; Dominici-Arosemena and Wolff, 2005). Correlations between (1) benthic variables and (2) fish densities and benthic covers were calculated using the Spearman Rank Correlation Coefficient.

Statistical analyses were conducted to compare temporal trends in fish composition and benthic cover before and after the hurricane, and to identify which fish species, or habitat variables, were driving any observed differences. This approach employed univariate (ANOVA and Fisher's post-hoc testing, Kruskal-Wallis tests) and multivariate (CA, PCA, RDA) tools.

The effects of the hurricane on benthic composition and fish assemblage features (e.g., species richness, fish abundances and trophic group abundance) were tested using one-way analysis of variance (ANOVA). If the ANOVA results indicated significant differences between the four sampling dates (probability level 0.05), the Tukey multiple comparison test was used to identify the significant differences. Prior to the analyses, data were tested for homogeneity of variance using Shapiro-Wilk's test and transformed when heterogeneous (Log$_{10}$ (x+1) for fish data; arcsine square-root for benthic cover data). If data were not homogeneous, non-parametric analysis of variance (Kruskal-Wallis test) was used to detect significant differences.

The potential shift in benthic composition was examined using a principal component analysis (PCA). All values of benthic group covers were arcsine square-root transformed and standardized to equal mean and standard deviation. In the figures, only the centroid of each sampling period has been shown (each one relates to 6 transects). A correspondence analysis (CA) was conducted using transect-densities of the fish species to study community structure changes. A $\log_{10}$ (x+1) transformation was applied to simplify the projections of the objects (transects) and the descriptors (species) on the factor axis. As for the benthic variables the centroid of each period of sampling has been shown in the figures (each one relates to 6 transects). To investigate the temporal changes within the fish communities in relation to the impacted habitats, an ordination analysis was performed. A preliminary detrended correspondence analysis applied to fish species abundance data revealed a slight gradient length (< 1 SD) suggesting that the species did not show a unimodal response to environmental gradients. According to the direct gradient technique (Ter Braak, 1996), a constrained linear ordination method, a redundancy analysis (RDA) was thus used (Ter Braak, 1986). Pre- and post-impact changes in fish species assemblages were investigated using Monte Carlo permutation tests within the framework of canonical correspondence analysis (Ter Braak, 1986).

Univariate analyses were performed using XLSTAT (version 2008.4.01) and multivariate analyses and figures using CANOCO and CANODRAW (version 4.51; Ter Braak and Smilauer, 2003).

RESULTS

Benthic communities

The percent cover of the major benthic categories obtained from the four sampling campaigns was analysed using PCA (Fig. 2). The first two dimensions described 41.5% of benthic group variability. The centroid of the date of the six transects for each sampling period pointed out a change in benthic cover with time according to the first axis (30.0% of the variability) with a stable transition phase between 3 and 8 months. This first axis is characterized by four vector loadings suggesting that live coral and rubble are inversely correlated to encrusting calcareous algae and macroalgae cover. The PCA results also revealed those coral species most impacted by the hurricane (left side of the graph) and those not affected (right side of the graph). Variability in live coral and macroalgae is orthogonal to the variability of turf and *Montastraea faveolata* (Ellis and Solander, 1786), indicating that these benthic components were not correlated.

Among all the benthic groups, only four categories of the PCA were significantly impacted by hurricane Dean: live coral, rubble, macroalgae and encrusting calcareous algae (Fig. 3). Live coral cover declined significantly from 37.3 ± 10.0% prior to the hurricane to 23.2 ± 4.7% in November 2008 (Kruskal-Wallis test, $p = 0.003$), resulting in 38% coral loss over the entire study period (Fig. 3). A rapid drop in coral cover was noticed in November 2007 (Mann-Whitney, U = 32.0, p = 0.024) showing the immediate impact of the hurricane. Thereafter, coral cover remained relatively stable. Rubble also significantly decreased gradually between the first and last samplings (ANOVA, F = 4.186, $p = 0.019$; Fig. 3). The decrease in coral cover was associated with a significant macroalgal bloom (doubled cover) in November 2007 (ANOVA, F = 7.724, p = 0.001). The coral/macroalgae balance became stable by April 2008 (Fig. 3). Live coral cover was negatively correlated to total cover of macroalgae and encrusting calcareous algae groups (Spear-

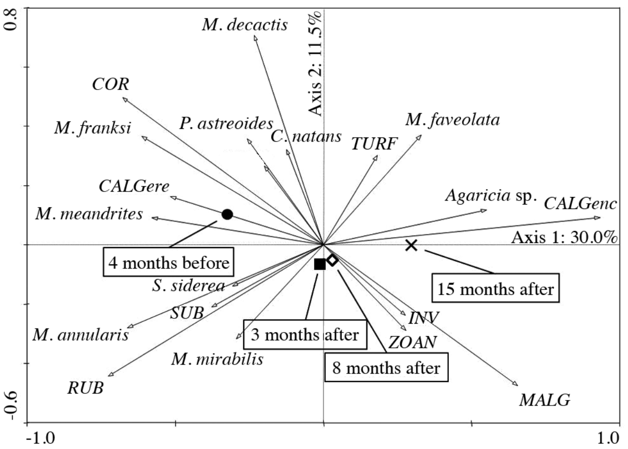

Figure 2. - Principal component analysis for transformed and standardized benthic cover data (arcsine, square-root). Variable loadings along the first two axes are presented as labelled vectors. Only species with absolute or relative contributions higher than 10% on one of the two first axes are displayed. Full names of each benthic category are given in table I.

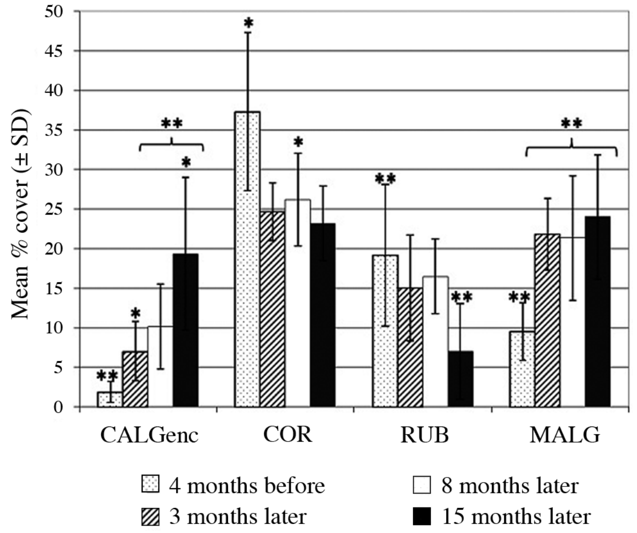

Figure 3. - Mean percent encrusting calcareous algae (CALGenc), coral (COR), rubble (RUB) and macroalgae (MALG) cover (%) at Jardin Tropical, Martinique (FWI), in surveys conducted 4 months before hurricane Dean (April 2007) and 3-8-15 months after hurricane Dean (November 2007-April 2008-November 2008). Error bars indicate one standard deviation. Significant results of pairwise comparison between sampling periods are noted (*: p < 0.05; **: p < 0.01).

man correlation coefficient: -0.758, $R^2 = 0.575$, $p < 0.0001$) but the weak R^2 value implies other explanatory confounding factors. The encrusting calcareous algae cover (Fig. 3) increased significantly (Kruskal-Wallis test, $p = 0.003$) and progressively during the study period.

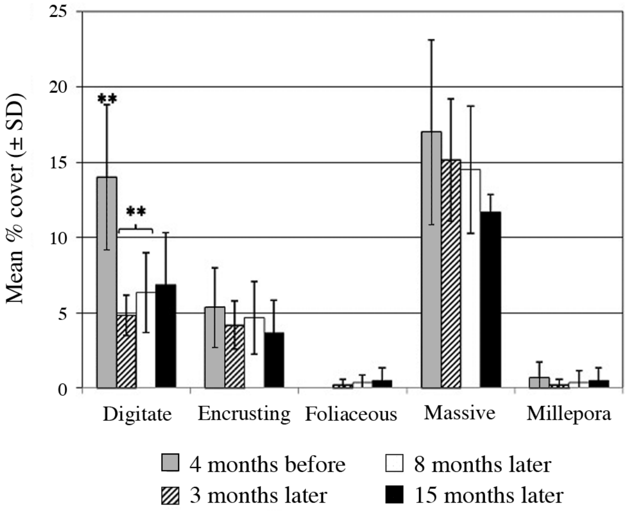

Figure 4. - Mean percent cover of the five coral morphological groups present at Jardin Tropical, Martinique, during surveys conducted 4 months (November 2007) before hurricane Dean and 3-8-15 months after hurricane Dean (November 2007-April 2008-November 2008). Error bars indicate one standard deviation. Significant results of pairwise comparison between sampling periods are noted (**: $p < 0.01$).

Seventeen coral species were identified during the study with a constant number of species of 13 to 15 for each sampling campaign. Species richness ranged from 6.8 ± 1.5 to 9.0 ± 1.3 species per transect according to the sampling periods but did not vary significantly with time (ANOVA, $F = 2.794$, $p = 0.067$).

The PCA results showed that many coral species were impacted by the hurricane (Fig. 2), except *M. faveolata* and *Agaricia sp.* Lamarck, 1801, but no significant difference was found when species-specific cover values were compared (Kruskal-Wallis test; $p > 0.05$).

To avoid species variability, coral species were clustered into growth-form groups (Fig. 4). The category most impacted by hurricane Dean was the digitate corals (ANOVA, $F = 7.604$, $p = 0.001$), which decreased by over 50% in November 2007. Massive coral cover decreased progressively during the study period, but not significantly (Kruskal-Wallis test, $p > 0.05$). No marked differences were observed for the other coral classes.

Fish communities

A total of 13,562 fishes were recorded during the study, belonging to 71 species (Tab. II). Species richness was identical in April and November 2007 (46 species) whereas it had increased up to 54 species by November 2008 (15

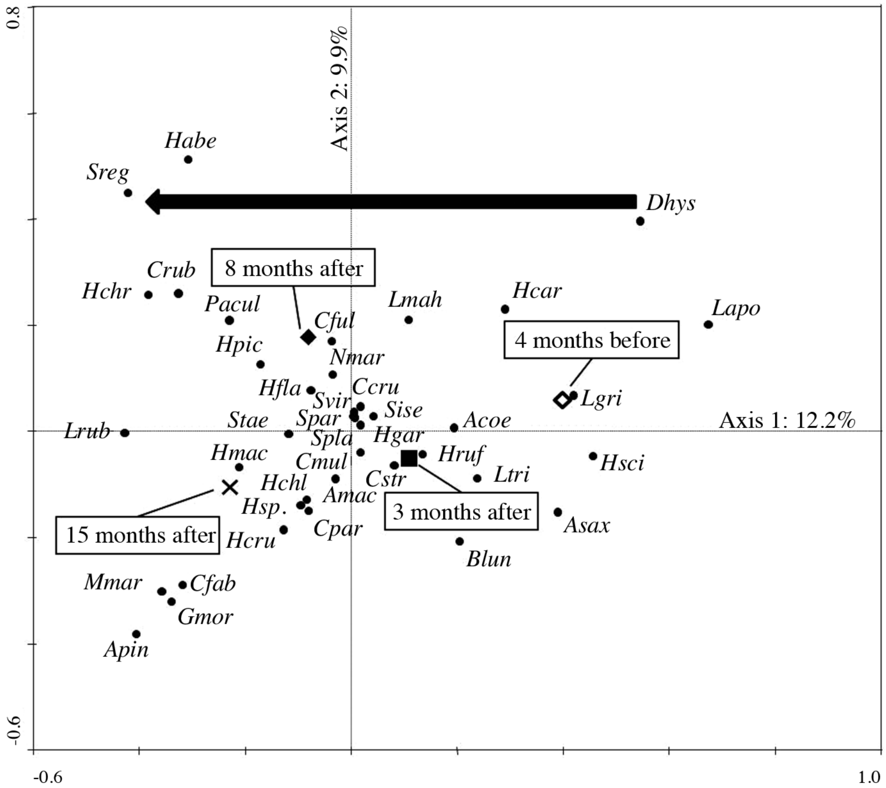

Figure 5. - Projection of transects on the first two axes determined by correspondence analysis. Only the barycenters of all transects of the same sampling period are shown (◊: transects sampled 4 months before hurricane Dean - April 2007, ■: transects sampled 3 months after - November 2007, ♦: transects sampled 8 months after - April 2008, ×: transects sampled 15 months after - November 2008). The percentages of total variance explained by the axes are given. Only species with absolute or relative contributions > 10% on one of the two first axes are shown. The arrow shows the direction of the fish community structure evolution. Full names of fishes are given in table II.

Table II. - Mean fish density (N.m^{-2} ± SD) for each sampling period, before and after hurricane Dean, in the survey site Jardin tropical, Martinique. The codes used in the multivariate analysis for each species and trophic group are indicated (Pk: Planktivore; RH: Roving Herbivore; TH: Territorial Herbivore; SI: Sessile Invertebrate Feeder; MI: Mobile Invertivore; O: Omnivore; C: Carnivore; Pi: Piscivore).

Family/Species	Codes		Mean densities ± one standard deviation			
	Species	Trophic groups	April 2007 (4 months before)	November 2007 (3 months after)	April 2008 (8 months after)	November 2008 (15 months after)
Acanthuridae						
Acanthurus bahianus Castelnau, 1855	A bah	RH	0.8 ± 1.3	1.8 ± 1.5	1.2 ± 0.8	1.5 ± 0.8
Acanthurus coeruleus Bloch & Schneider, 1801	A coe	RH	1.5 ± 0.5	0.3 ± 0.5	0.3 ± 0.8	0.3 ± 0.5
Aulostomidae						
Aulostomus maculatus Valenciennes, 1837	A mac	Pi	0.7 ± 0.8	1.3 ± 1.4	1.3 ± 1.4	1.7 ± 1.4
Bothidae						
Bothus lunatus (Linnaeus, 1758)	B lun	C	0.3 ± 0.5	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
Carangidae						
Carangoides ruber (Bloch, 1793)	C rub	Pi	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.3 ± 0.5
Chaetodontidae						
Chaetodon capistratus Linnaeus, 1758	C cap	SI	0.5 ± 0.8	1.0 ± 1.1	0.8 ± 1.2	0.5 ± 0.5
Chaetodon striatus Linnaeus, 1758	C str	SI	0.2 ± 0.4	0.0 ± 0.0	0.2 ± 0.4	0.2 ± 0.4
Prognathodes aculeatus (Poey, 1860)	P acul	SI	0.0 ± 0.0	0.2 ± 0.4	0.3 ± 0.5	0.3 ± 0.5
Cirrhitidae						
Amblycirrhitus pinos (Mowbray, 1927)	A pin	MI	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.0 ± 1.7
Diodontidae						
Diodon hystrix Linnaeus, 1758	D hys	MI	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Ephippidae						
Chaetodipterus faber (Broussonet, 1782)	C fab	MI	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.8
Haemulidae						
Haemulon carbonarium Poey, 1860	H car	MI	0.3 ± 0.5	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
Haemulon chrysargyreum Günther, 1859	H chr	MI	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.8	0.5 ± 0.8
Haemulon flavolineatum (Desmarest, 1823)	H fla	MI	0.2 ± 0.4	1.2 ± 0.4	2.0 ± 1.1	1.2 ± 1.2
Haemulon plumierii (Lacepède, 1801)	H plu	MI	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0
Haemulon sciurus (Shaw, 1803)	H sci	MI	0.7 ± 1.2	0.5 ± 0.8	0.0 ± 0.0	0.2 ± 0.4
Holocentridae						
Holocentrus rufus (Walbaum, 1792)	H ruf	MI	0.7 ± 1.0	0.7 ± 0.8	0.3 ± 0.5	0.2 ± 0.4
Myripristis jacobus Cuvier, 1829	M jac	Pk	11.7 ± 8.6	42.7 ± 18.2	30.2 ± 17.4	23.5 ± 10.5
Neoniphon marianus (Cuvier, 1829)	N mar	MI	0.3 ± 0.5	0.5 ± 0.5	1.0 ± 0.9	0.5 ± 0.5
Sargocentron vexillarium (Poey, 1860)	S vex	MI	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
Inermiidae						
Inermia vittata Poey, 1860	I vit	Pk	0.0 ± 0.0	0.0 ± 0.0	1.7 ± 4.1	0.0 ± 0.0
Labridae						
Bodianus rufus (Linnaeus, 1758)	B ruf	MI	0.5 ± 0.8	0.0 ± 0.0	0.2 ± 0.4	0.2 ± 0.4
Clepticus parrae (Bloch & Schneider, 1801)	C par	Pk	15.7 ± 31.9	10.0 ± 7.3	31.7 ± 68.2	72.7 ± 79.3
Halichoeres garnoti (Val. in Cuv. and Val., 1839)	H gar	MI	24.0 ± 7.0	20.3 ± 7.9	20.3 ± 7.4	24.3 ± 12.5
Halichoeres maculipinna (Müller & Troschel, 1848)	H mac	MI	0.0 ± 0.0	2.0 ± 1.8	1.0 ± 1.7	4.7 ± 2.4
Halichoeres pictus (Poey, 1860)	H pic	MI	0.7 ± 1.0	0.3 ± 0.8	4.7 ± 6.4	7.3 ± 13.0
Halichoeres radiatus (Linnaeus, 1758)	H rad	MI	0.0 ± 0.0	0.3 ± 0.8	0.0 ± 0.0	0.2 ± 0.4
Thalassoma bifasciatum (Bloch, 1791)	T bif	Pk	31.0 ± 21.5	45.3 ± 14.5	36.0 ± 19.7	36.7 ± 21.2
Lutjanidae						
Lutjanus apodus (Walbaum, 1792)	L apo	C	0.5 ± 0.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

Table II. - Continued.

Family/Species	Codes		Mean densities ± one standard deviation			
	Species	Trophic groups	April 2007 (4 months before)	November 2007 (3 months after)	April 2008 (8 months after)	November 2008 (15 months after)
Lutjanus griseus (Linnaeus, 1758)	L gri	C	0.3 ± 0.8	0.5 ± 1.2	0.0 ± 0.0	0.0 ± 0.0
Lutjanus mahogoni (Cuvier, 1828)	L mah	C	1.0 ± 0.9	0.3 ± 0.5	0.8 ± 1.0	0.2 ± 0.4
Ocyurus chrysurus (Bloch, 1791)	O chr	C	1.0 ± 1.1	0.5 ± 0.5	0.3 ± 0.8	0.7 ± 0.8
Monacanthidae						
Cantherhines macrocerus (Hollard, 1853)	C mac	O	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
Cantherhines pullus (Ranzani, 1842)	C pul	O	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.5	0.0 ± 0.0
Mullidae						
Mulloidichthys martinicus (Cuvier, 1829)	M mar	MI	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.5
Muraenidae						
Gymnothorax miliaris (Kaup, 1856)	G mil	C	0.2 ± 0.4	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
Gymnothorax moringa (Cuvier, 1829)	G mor	Pi	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.5
Ostraciidae						
Lactophrys bicaudalis (Linnaeus, 1758)	L bic	SI	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
Lactophrys triqueter (Linnaeus, 1758)	L tri	O	0.3 ± 0.5	0.2 ± 0.4	0.0 ± 0.0	0.2 ± 0.4
Pomacanthidae						
Holacanthus ciliaris (Linnaeus, 1758)	H cil	SI	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
Pomacentridae						
Abudefduf saxatilis (Linnaeus, 1758)	A sax	O	1.3 ± 3.3	0.3 ± 0.8	0.3 ± 0.8	0.3 ± 0.5
Chromis cyanea (Poey, 1860)	C cya	Pk	102.7 ± 103.1	38.0 ± 31.0	44.7 ± 55.0	85.7 ± 49.6
Chromis multilineata (Guichenot, 1853)	C mul	Pk	64.3 ± 76.9	124.3 ± 47.6	120.7 ± 76.4	77.3 ± 39.4
Microspathodon chrysurus (Cuvier, 1830)	M chr	TH	1.0 ± 1.7	1.3 ± 1.0	0.7 ± 1.0	0.3 ± 0.8
Stegastes adustus (Troschel, 1865)	S adu	TH	0.7 ± 1.6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Stegastes leucostictus (Müller & Troschel, 1848)	S leu	TH	3.3 ± 2.7	11.7 ± 5.9	12.0 ± 2.2	14.7 ± 5.3
Stegastes partitus (Poey, 1868)	S par	TH	103.3 ± 50.9	109.7 ± 48.0	133.0 ± 20.7	133.3 ± 19.6
Stegastes planifrons (Cuvier, 1830)	S pla	TH	62.7 ± 13.1	76.3 ± 13.9	91.3 ± 15.4	82.7 ± 7.2
Priacanthidae						
Heteropriacanthus cruentatus (Lacepède, 1801)	H cru	MI	0.0 ± 0.0	0.2 ± 0.4	0.3 ± 0.5	0.3 ± 0.5
Scaridae						
Scarus iseri (Bloch, 1789)	S ise	RH	22.0 ± 7.6	27.0 ± 11.1	16.2 ± 6.5	10.0 ± 3.0
Scarus taeniopterus Desmarest, 1831	S tae	RH	3.0 ± 4.4	5.8 ± 8.0	10.2 ± 11.1	18.2 ± 7.3
Scarus vetula Bloch & Schneider, 1801	S vet	RH	0.3 ± 0.8	0.5 ± 0.8	0.7 ± 1.2	0.0 ± 0.0
Sparisoma atomarium (Poey, 1861)	S ato	RH	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.8	0.0 ± 0.0
Sparisoma aurofrenatum (Val. in Cuv. and Val., 1840)	S aur	RH	2.2 ± 0.8	2.2 ± 1.6	1.7 ± 1.0	6.0 ± 2.1
Sparisoma rubripinne (Val. in Cuv. and Val., 1840)	S rub	RH	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Sparisoma viride (Bonnaterre, 1788)	S vir	RH	4.3 ± 2.1	6.8 ± 3.6	6.0 ± 1.4	5.8 ± 2.1
Sciaenidae						
Equetus punctatus (Bloch & Schneider, 1801)	E pun	MI	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Scombridae						
Scomberomorus regalis (Bloch, 1793)	S reg	Pi	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
Serranidae						
Cephalopholis cruentata (Lacepède, 1802)	C cru	C	3.3 ± 1.2	3.3 ± 1.0	3.8 ± 1.2	3.8 ± 2.4
Cephalopholis fulva (Linnaeus, 1758)	C ful	C	0.5 ± 1.2	0.5 ± 0.5	0.3 ± 0.5	0.2 ± 0.4
Epinephelus guttatus (Linnaeus, 1758)	E gut	C	0.0 ± 0.0	0.3 ± 0.5	0.0 ± 0.0	0.0 ± 0.0

Table II. - Continued.

Family/Species	Codes		Mean densities ± one standard deviation			
	Species	Trophic groups	April 2007 (4 months before)	November 2007 (3 months after)	April 2008 (8 months after)	November 2008 (15 months after)
Hypoplectrus aberrans Poey, 1868	H abe	C	0.0 ± 0.0	0.0 ± 0.0	1.3 ± 2.4	1.0 ± 1.7
Hypoplectrus chlorurus (Cuvier, 1828)	H chl	C	1.3 ± 2.1	1.3 ± 1.6	1.0 ± 1.1	2.0 ± 1.8
Hypoplectrus guttavarius (Poey, 1852)	H gut	C	0.0 ± 0.0	0.7 ± 1.0	0.3 ± 0.8	0.0 ± 0.0
Hypoplectrus nigricans (Poey, 1852)	H nig	C	0.0 ± 0.0	0.3 ± 0.8	1.3 ± 1.0	0.0 ± 0.0
Hypoplectrus puella (Cuvier, 1828)	H pue	C	2.0 ± 1.8	1.3 ± 1.6	1.3 ± 1.6	1.3 ± 1.0
Hypoplectrus sp. - Hybrid	H sp.	C	0.7 ± 1.6	1.3 ± 1.6	0.7 ± 1.0	1.7 ± 1.5
Liopropoma rubre Poey, 1861	L rub	MI	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.5
Serranus tigrinus (Bloch, 1790)	S tig	MI	0.0 ± 0.0	1.7 ± 1.5	1.3 ± 1.6	3.3 ± 3.9
Synodontidae						
Synodus intermedius (Spix & Agassiz, 1829)	S int	Pi	0.3 ± 0.5	0.0 ± 0.0	0.3 ± 0.5	0.5 ± 0.5
Tetraodontidae						
Canthigaster rostrata (Bloch, 1786)	C ros	SI	3.7 ± 3.2	9.0 ± 6.5	7.3 ± 4.7	7.0 ± 3.5

months later). This trend was noticed for the mean species richness values per transect, which varied significantly from 23.7 ± 4.4 species (4 months before-event-April 2007) to 29.7 ± 2.9 species (15 months post-event-November 2008) (Kruskal-Wallis test, $p = 0.017$).

The mean fish density calculated in April 2007 before the hurricane was 477 ± 157 ind.200 m^{-2} and compared to 637 ± 186 ind.200 m^{-2} in November 2008, but this difference was not significant (ANOVA, $F = 1.196$, $p > 0.05$) due to large fluctuations in planktivorous species densities (between 10 and 66% of the total number of fishes). These species were then removed from the data set and a one-way ANOVA was performed revealing a significant increase in mean fish density with time ($F = 7.963$, $p = 0.001$).

A correspondence analysis was performed on fish density for each transect before and after the hurricane to investigate a possible impact on fish community structure (Fig. 5). The projection of the transects on the first two axes (axes 1 and 2: 22.1% of the total inertia) isolated the four sampling periods (April-November 2007; April-November 2008) along the first axis, from right to left, showing a change in community structure during the 20 months of the study. While globally a large part of the population was not affected by the hurricane (centre of figure 5), some species such as *Lutjanus apodus* (Walbaum, 1792), *L. griseus* (Linnaeus, 1758), *Diodon hystrix* Linnaeus, 1758 and *Haemulon sciurus* (Shaw, 1803) decreased in number of individuals and/or disappeared from the surveys entirely (species on the right side of axis 1). Conversely, other species that were absent or present in few numbers in April 2007 before the hurricane, such as *Haemulon chrysargyreum* Günther, 1859, *Mulloidichthys martinicus* (Cuvier, 1829) and *Amblycirrhitus pinos* (Mowbray, 1927), were well established and/or their number increased after the hurricane in November 2008 (species on left side of axis 1).

A redundancy analysis was performed on the species-transects matrix to investigate the correlation between damages to the benthic community and fish assemblages (Fig. 6). According to the RDA, the species-environment correlation values were 0.868 and 0.843 for the two first axes, respectively. The first two eigenvalues displayed 24.0% of the total inertia (total variance in fish community composition), and 56.7% of the variance in the weighted average of species with the environmental variables. The Monte Carlo test results for the first and all canonical axes were significant ($p = 0.02$) demonstrating that coral cover significantly explains variability in fish structure (Monte Carlo test, $p = 0.012$). Similarly to the results found from PCA for benthic variables (Fig. 2), benthic composition changed with time along the axis MALG-COR, from right to left on axis1 (Fig. 6). Fish species community changed along the same ecological gradient from 4 months before (April 2007) to 15 months after hurricane Dean (November 2008) (correlation coefficient = 0.51 and -0.48 with the RDA axis 1 for COR and MALG respectively). A negative slope in coral cover against time appears on the ordination plane and is inversely correlated to macroalgae cover (correlation coefficient = -0.74). The second axis differentiated the fish community from each sampling period according to other habitat characteristics i.e., the gorgonian and the encrusting calcareous algae (RDA correlation coefficients on axis 2 = 0.54 and 0.41 respectively).

When looking at the fish densities by trophic groups, it appears that only the territorial herbivores experienced a significant population change after hurricane Dean (ANOVA, $F = 5.981$, $p = 0.004$). Abundance increased by a third

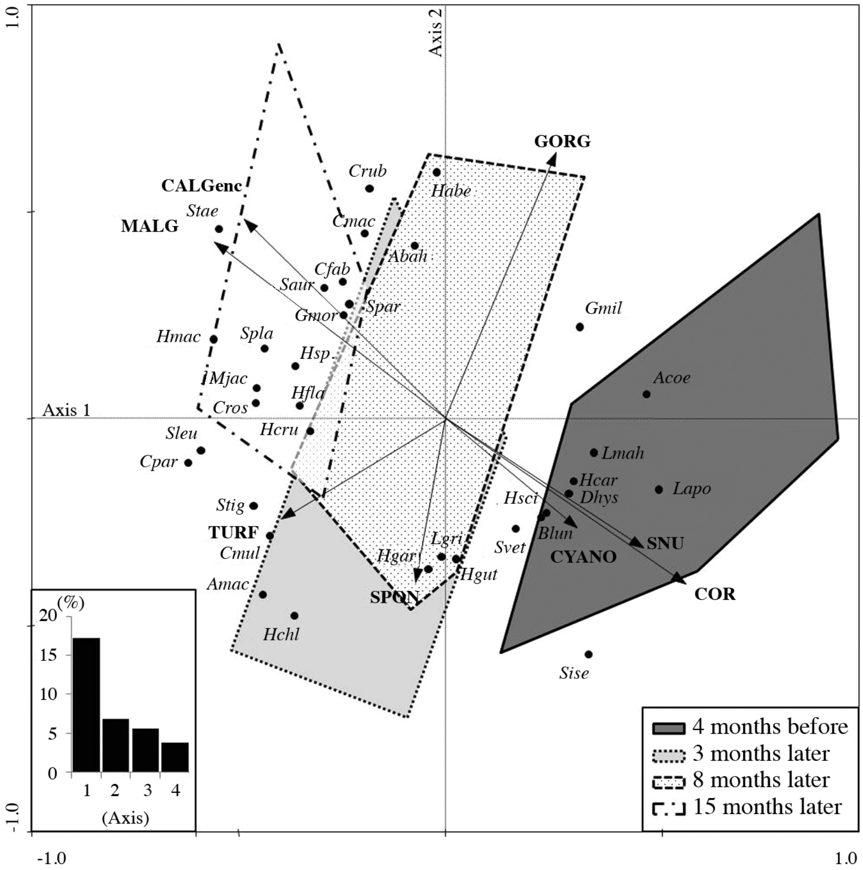

Figure 6. - Redundancy analysis (RDA) showing sample date scores grouped according to sampling periods by different polygons and fish species scores (full circles) along principal environmental gradients (arrows) (CALG enc = encrusting calcareous algae, COR = live coral, CYANO = cyanophycae, GORG = gorgonia, MALG = macroalgae, SPON = sponge, SNU = all types of bare substrate). Full names of fishes are given in table II. Histogram bars display eigenvalues (% of the variance in the weighted averages of the species with respect to each of the environmental variables) for the four first axes of the analysis.

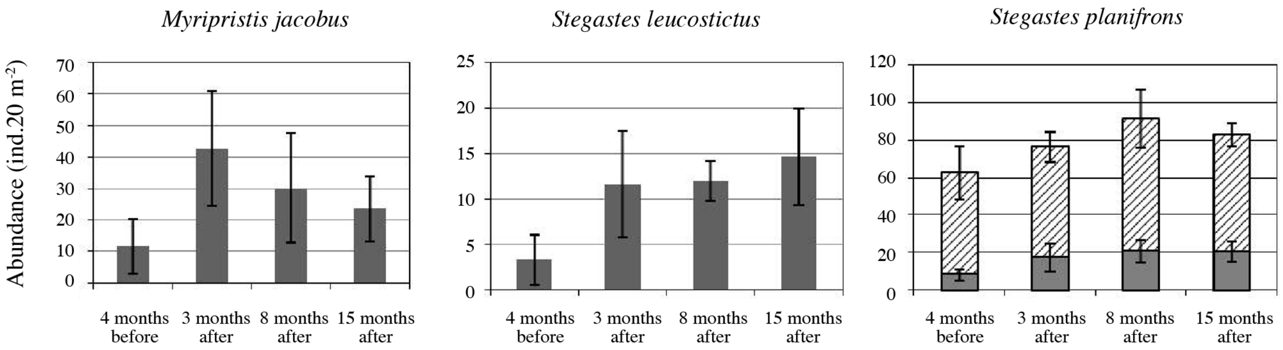

Figure 7. - Changes in the abundance values of *Myripristis jacobus*, *Stegastes leucostictus* and *S. planifrons*, before and after the hurricane Dean at the Jardin Tropical site, Martinique. A distinction is made between juveniles (solid) and adults (hatched) of *S. planifrons*.

(+35.1%). This increase was positively correlated to the rise in macroalgae and encrusting algae cover (Spearman correlation coefficient: 0.528, $R^2 = 0.279$, $p = 0.009$) while it was negatively correlated to live coral cover (Spearman correlation coefficient: -0.500, $R^2 = 0.250$, $p = 0.014$). Within this group, the densities of *Stegastes leucostictus* (Müller & Troschel, 1848) were low in April 2007 (3.3 ± 2.7 ind.200 m^{-2}; Fig. 7) and increased significantly by a factor of 3 in November 2008 (14.7 ± 5.3 ind.200 m^{-2}; Kruskal-Wallis test, $p = 0.008$). The abundance values of *Stegastes planifrons* (Cuvier, 1830) (Fig. 7) were significantly increased by 30% for the same period (Kruskal-Wallis test, $p = 0.014$) due to a rise in juvenile abundance (Kruskal-Wallis test, $p = 0.006$). The macroalgae and encrusting algae covers positively affected *S. leucosticus* abundance (Spearman correlation coefficient: 0.639, $R^2 = 0.409$, $p = 0.001$), while live coral cover was negatively correlated to abundance (Spearman correlation coefficient: -0.636, $R^2 = 0.405$, $p = 0.001$).

Although no significant differences between density values could be found for the planktivorous trophic group, *Myripristis jacobus* Cuvier, 1829 underwent strong density fluctuations between April 2007 and November 2008 starting from a value of 11.7 ± 8.6 ind.200 m^{-2} in April 2007, increasing to 42.7 ± 18.2 ind.200 m^{-2} in November 2007, and finally decreasing to 23.5 ± 10.5 ind.200 m^{-2} by November 2008 (Fig. 7).

All these significant results were only found at Jardin Tropical. No similar changes were observed on any other monitored site.

DISCUSSION

Hurricane damage to coral reefs can be highly variable according to many parameters (e.g., Harmelin-Vivien and Laboute, 1986; Bythell *et al*., 2000; Gardner *et al*., 2005; Álvarez-Filip and Gil, 2006). Hurricane Dean was the strongest tropical hurricane of the 2007 Atlantic season (Category 5 storm). Although it was only a Category 2 when it impacted Martinique, the associated swells critically affected the Southern Caribbean reefs. Only 3 months after this event, a 38% coral cover decline was observed while macroalgae cover had doubled. A gradual increase in encrusting calcareous algae cover was also observed over time. Fifteen months after the hurricane the structure and composition of the studied reef sites did not show any sign of recovery. The opportunistic benthic organisms associated with reef degradation persisted and have continued to colonize the site under the current environmental conditions. Similar algal cover development resulting from a hurricane event has been documented by Cheal *et al*. (2002) in Australia, suggesting that this colonization is the consequence of an increase in suitable substrate once corals have died. According to Gardner *et al*. (2005), coral cover is reduced, on average, by 17% following a Caribbean hurricane event. A 38% coral cover loss was observed throughout our study period, highlighting the strength and devastating effect of hurricane Dean on this site of Martinique's southern reefs.

However, the decrease in coral cover was not statistically significant at the species level, due to low cover values and large variance among transects. Consequently, only trends could be drawn at the species level and different coral species were impacted in different ways by the hurricane. Nevertheless, significant differences were noticed among coral growth-form groups. Major damage was observed in digitate corals (*Madracis mirabilis*, *M. decactis*), whereas massive corals such as *M. faveolata* were less impacted. These results agree with other studies, which show that the tolerance of hard corals to storms varies according to their form with branching and digitate forms being more susceptible to damage than massive forms (Woodley *et al*., 1981; Rogers, 1993; Harmelin-Vivien, 1994). However, a delayed effect of the hurricane was observed in the massive coral species, *M. annularis,* in November 2008. This phenomenon has previously been observed in the Caribbean (Knowlton *et al*., 1981). Colonies of *M. annularis* grow vertically and develop a vast number of columns where only the top of columns are alive and the base is composed of dead coral skeleton. These relatively unsteady compacted structures have been destroyed by swells and entire blocks have been transported by strong water movement. Displacement of these large pieces has caused substantial mechanical damage to smaller surrounding corals (Woodley *et al*., 1981; Edmunds and Witman, 1991; Cheal *et al*., 2002) and has reconfigured live parts of the reef edifice. This new structural organization might have been the cause of delayed mortality as living parts of the coral are exposed to abrasion and smothering, are more accessible to predators and are more susceptible to disease, fragmentation and stress (Knowlton *et al*., 1981).

Despite this rapid decrease in coral cover, no species completely disappeared from the site as a result of the climatic event. Half of the coral species surveyed in Martinique by Bouchon and Laborel (1986) were recorded during this study. The hurricane did not have a negative effect on either species richness or digitate species, such as *M. mirabilis,* which already seems to be growing and recolonizing the reef (Martinique IFRECOR coral reef monitoring program, unpubl. data). The relatively rapid growth of this species, varying between 6 and 12 mm according to site conditions (Nagelkerken *et al*., 2000), could explain the slight increase in digitate coral cover 15 months after the hurricane.

While many studies have shown an important increase in rubble after a hurricane (Harmelin-Vivien and Laboute, 1986; Adams and Ebersole, 2004; Álvarez-Filip and Gil, 2006), a decrease in the percent cover of rubble was observed after hurricane Dean, which intensified after several months. The initial rubble decline (3 months after the hurricane) could be attributed to hurricane wave action, removing loose material. Whereas subsequent rubble decrease could be related to the progressive increase in encrusting calcareous algae that slowly colonized rubble and recently dead coral.

Hurricane Dean affected coral reef fish assemblages soon after its impact, as seen in changes in the total abundance, assemblage structure, species richness, and abundance of selected species over the study period. The number of non-cryptic fish species rose from 46 to 54 species. Several rare species (*L. apodus* and *D. hystrix*) that were observed during pre-hurricane surveys were not recorded in the post-hurricane counts and species that had never been seen before hurricane Dean were observed following its impact. Kaufman (1983) and Walsh (1983) had already noticed that certain fish species, which leave a site during a storm, return a few months later. In this study, some species may have temporarily disappeared however they were not observed in the last survey at "Jardin Tropical". These species have not yet reappeared and may have relocated to adjacent reefs, but confirmation is required. Other opportunistic species, such as *Stegastes planifrons* and *S. leucostictus,* have permanently settled at “Jardin Tropical”, taking advantage of the habitat’s reorganization and its loss of coral reef complexity by colonizing new spaces and reproducing. The trend of increased Pomacentridae abundance was already observed in previous studies evaluating the effects of hurricanes on reef fish populations (Letourneur *et al.*, 1993; Lewis, 1998). McClanahan *et al.* (1999) showed that under certain disturbances, such as intense fishing resulting in a decline in predators, small fishes such as damselfish, can benefit and colonize new habitats. Other disturbances such as hurricanes could generate a similar response and could explain the density changes observed for the Pomacentridae. The two species of the genus *Stegastes*, *S. leucostictus* and *S. planifrons*, are dominant, territorial and solitary damselfishes, abundant in Martinique crest reefs at a depth of 10 m (Lawson *et al.*, 1999; Haley and Müller, 2002). Individuals of these species maintain their territory by farming and displaying aggression toward other fishes (Ceccarelli *et al.*, 2001). Damselfishes bite the substrate to prevent other organisms and algae from growing over their habitat, including live coral (Kaufman, 1977; Montgomery, 1980; Hata and Kato, 2003). Damselfishes are so aggressive that they can affect the spatial distribution of fish species (Jones, 2005) in such a way that other species, such as Acanthuridae, avoid the damselfish territories (Risk, 1998). Our study confirms this effect as *Acanthurus coeruleus* Bloch & Schneider, 1801 was no longer present in the post-hurricane survey at “Jardin Tropical”.

Lewis (1986) and Morrison (1988) reported a rapid reduction in the biomass and diversity of algal assemblages due to intense grazing by other herbivores after they had removed damselfish from their territories. The increase in damselfish populations at “Jardin Tropical” could explain the absence of previously observed species that would have normally reappeared after the hurricane. It has also been stated that individuals establish territories very early during post-settlement and early adulthood (Doherty, 1983; Kaufman *et al.*, 1992; Letourneur, 2000). In Martinique, the settlement phase of these two species occurs in September-October (McGehee, 1995), which is about one month after hurricane Dean hit in August 2007. This timing would explain the increase in their abundance and the rapid spread of macroalgae communities.

The profound modification of the reef habitat structure caused by hurricane Dean also impacted soldierfish, *M. jacobus*, which is a ubiquitous species among Martinique’s shallow reefs. This planktivorous species resides in the shelter of coral edifices during the day and has a predominantly nocturnal feeding behavior (Wyatt, 1983). When coral structures were destroyed during the hurricane, numerous individuals were dislodged from their shelters, which may explain their increase in density in November 2007. The decrease in density values thereafter could be the result of both predation and new available shelters.

Hurricanes rarely result in direct fish mortality (Walsh, 1983; Bell and Hall, 1994; Nagelkerken *et al.*, 2005) but most fishes depend on coral reef habitat for vital resources such as food, shelter and living space, all of which are essential to their survival and reproduction (Jones and Syms, 1998; Öhman and Rajasuriya, 1998; Steele, 1999). As shown in our study and those by other authors, fish species richness and fish abundance were positively correlated with habitat complexity, microhabitat type and live coral cover (Carpenter *et al.*, 1981; Hixon and Beets, 1993; Friedlander and Parrish, 1998; Holbrook *et al.*, 2002; Wilson *et al.*, 2007). The decline in coral cover negatively affected species that live in close contact with coral colonies (*M. jacobus* in Martinique), but positively affected herbivorous species that benefit from shifts to macroalgae (Lewis, 1998). Following such a disturbance, reef fish communities often reorganize themselves due to the ensuing competition for food and space. During this reorganization some genera, such as *Stegastes* in our case, increase in density (Williams, 1984; McClanahan *et al.*, 1999) and accentuate the hurricane’s impact on coral mortality by supporting the settlement and development of algae (Hixon and Beets, 1993; Ceccarelli *et al.*, 2001).

The scientific community is divided when it comes to the main factors involved in coral reef degradation. While some authors suggest that catastrophic physical disturbances such as hurricanes constitute the major factor inducing massive coral death (Bak and Luckhurst, 1980), others impute reef degradation to coral disease, bleaching (Bythell *et al.*, 1993; Hughes *et al.*, 2003) and overfishing (Pandolfi *et al.*, 2003). Other authors attribute this decline to eutrophication and nutrient enrichment (Lapointe *et al.*, 2004). Aronson *et al.* (2003) proposes that the causes vary with geographical location and that disease and hurricanes are the main forces of degradation in the Caribbean. In 2005, Gardner *et al.* specified that while hurricanes contribute to Caribbean reef degradation, there are other stressors that have more considerable consequences on coral reefs. Obviously, long-term coral reef degradation is caused by the successive and cumulative effects of many factors. Today, it is acknowledged that combined natural and human pressures encourage the decline of coral reefs throughout the world (Hughes, 1994; Hodgson, 1999; Hughes *et al.*, 2003; Bellwood *et al.*, 2004; Chabanet *et al.*, 2005). In general, reefs with few anthropogenic stressors can recover after a hurricane (Connell *et al.*, 1997). When marine pollution is as significant as it is in Martinique (e.g., Littler *et al.*, 1992; Bocquené and Franco, 2005; Coat *et al.*, 2006) and most of the Caribbean islands, complete recovery of coral reefs to their untouched state becomes unrealistic. The rapid spread of macroalgae observed in this study (cover rose from 9.5% to 21.8% in 3 months) could be explained by marine coastal eutrophication and/or by insufficient control of macroalgal growth by grazers (Lirman, 2001; Mantyka and Bellwood, 2007), highlighting the coastal overfishing problem in Martinique.

An annual monitoring of the “Jardin Tropical” site, using the same protocol, will evaluate the ability of the reef to recover from the damages caused by hurricane Dean.

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